Introduction to 'The Nature of the Sexes'

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The Nature of the Sexes: The Sociobiology of Sex Differences and the 'Battle of the Sexes

Introduction to *The Nature of the Sexes*

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> ".. we have evolved a nervous system that acts in the interests of our gonads, and one attuned to the demands of reproductive competition. If fools are more prolific than wise men, then to that degree folly will be favored by selection. And if ignorance aids in obtaining a mate, then men and women will tend to be ignorant" (Ghiselin, 1974).

That the human brain developed in the service of the gonads, and not to solve academic riddles and cross-word puzzles, may at first sight seem an unusually provocative and even offensive statement by an alienated armchair theorist. We usually grant that our sexually dimorphic bodies – our anatomical, morphological, physiological and neuroendocrine features and characteristics – may have evolved ***also*** in the service of procreation (after all, we are not sexually dimorphic just for the fun of it), but our precious brains... our mental faculties... our very mind and soul? Yet, a moment's reflection reveals that this must indeed be so. The only currency in the cold calculus of evolution is reproductive success: the differential contribution of individuals to the gene pool of the population. That is what is called natural selection ever since Darwin. Those who do not contribute drop out of the race and their genes vanish with them (Humans can, of course, more or less consciously and deliberately decide to drop out). Those who do contribute pass on their genes to future generations and may enjoy the prospect of genic immortality. Considering what is at stake, one may deduce that those genes that have not 'programmed' their temporary vehicles with strong urges to reproduce have been selected against since time immemorial.

Reproductive success, thus, is the name of the game, and our individual reproductive success depends on how clever, smart or intensive we play the game. I use the term 'clever' and 'smart' here deliberately, because I mean 'clever and smart in relation to the rules of the game'; there is no intelligence or intent or even consciousness involved (though in the human case some social intelligence may come in handy, as may good looks, and status and money, and whatever is considered attractive by the opposite sex).

And, as will be seen later on, because there are different Grand Strategies, Gambits and Tactics for males and females in the Differential Reproduction Game, it must follow that the brain not only evolved 'attuned to the demands of reproductive competition', but also that the brain belonging to the sexually dimorphic bodies must itself be sexually dimorphic too. It would be highly negligent of nature if this were not the case. (I use the word 'brain' here as a shorthand for the neurological as well as the psychological/mental equipment we are fed up with).

That the human species comes in two flavors or varieties – male and female – is a fact of life some people regret, and others welcome and enjoy: "Vive la petite différence". And that differences between the sexes are not confined to the obvious anatomical and morphological ones, but also encompass brain functioning and behaviour, is probably known since the dawn of mankind, but only recently being acknowledged and incorporated into scientific theorizing. And only gradually are we unravelling the evolutionary rationale behind these differences.

At this point some clarification of concepts is in order. I shall use the concepts of 'female' and 'male' in a more biological sense (and for the sake of argument suppose that an organism

is either female or male – excluding, for the time being, the cases of intersexuality, (pseudo)hermaphroditism, transsexuality, etc.). To all practical purposes, this is a fair assumption, especially since persons who are both or neither are nonetheless raised as either female or male in most human societies, and acquire and display the characteristics which we generally refer to as 'feminine' or 'masculine'. What do we mean when we talk about feminine and masculine? Generally, these are qualities (or the lack of them) we ascribe and attribute to the bearers of the two varieties of gonads: when ***it*** has ovaries and a vagina, ***it*** is female and supposed to exhibit feminine behaviour; when ***it*** has testes and a penis, ***it*** is male and supposed to display masculine characteristics. These 'gender' attributions, which function as much as ***pre***scriptions (ideas and rules about how men and women ought to behave, think and feel), are culturally acquired stereotypes adhering to the social role models of women and men in a particular society at a particular time – 'gender' itself being a cultural and historical construction. Much of it is rather arbitrary and fluctuates according to the fashion of the day. But not infinitely so. There is some kernel of (biological) invariance which can hardly be transcended. For example, parents do not have to coerce or coax boys to play with toy weapons, and parents do not have to force or teach girls to play with dolls. In other words, there is no infinite plasticity; there are limits to the behavioural malleability of the sexes. The reason behind that is really quite simple: it would be highly negligent of evolution (or Nature, or God) to create a sexually dimorphic species without at the same time 'programming' or 'wiring', or otherwise preparing the individuals for the divergent strategies, functions and roles they have to play during their lifetimes, especially in the reproductive domain, as will be seen shortly. All this is not meant to imply that the envisaged sex differences are in any way 'absolute'. For example, many mammalian species are quite capable of heterotypical sexual behaviour (i.e. behaviour properly 'belonging' to the other sex), although such behaviour is generally more common in females. In this volume, Peter Meyer, from the university of Augsburg, Germany, will explore the cultural construction of sex identities in more detail. In the view of evolutionary biology, organisms are just temporary vehicles with only one purpose: to transmit their genes to future generations. The organism is ephemeral and mortal. The genes are, in principle, immortal and have the 'selfish' interest in spreading as many copies of themselves as possible. Here is where the 'strategy of the genes' comes in.

But let us return for a moment to the issues of sex and gender, and the inescapable biological determination many people feel to be associated with these categories. For the time being it seems sensible to state that gender differences always presuppose some sex differences.

An important distinction in evolutionary biology, indeed in any attempt to explain animal and human behaviour, is that between ***ultimate*** (or evolutionary, of phylogenetic) and ***proximate*** (or immediate, or ontogenetic) causes. Succinctly stated: proximate explanations address the ***how*** of a behaviour, ultimate explanations ***why*** it occurs at all.

A proximate explanation considers the short- and longer-term causation of that behaviour in psychological or neurophysiological terms (e.g., psychological states, motivations, previous experience, stimulus configurations, etc.). An ultimate explanation would ask: why did this particular behaviour evolve? Did it confer fitness advantages in the past to the bearer of this particular set of genes?

Many critics of sociobiology and, indeed, many sociobiologists themselves often fail to distinguish these levels-of-explanation. The proximate cause of a certain sexual behaviour may be, for example, the seeking of the thrill of orgasm with a specific partner, 'libido', or whatever we call the urge. An ultimate approach would address the question how and why in

(human) phylogeny sex ever developed: why was it selected?, had it survival value?, did it contribute to inclusive fitness?, did it lead to greater reproductive success in those species that practised it than in those species that did not have it in their behavioural repertoire?

These and similar questions invoke ‘natural selection’.

“Natural selection can honestly be described as a process for the maximization of short-sighted selfishness” as Williams (1988) states, but as the principle of kin-selection suggests, we are equally selected to be (short-sighted or not) nepotistically altruistic. Natural selection operates through the differential reproductive success of individual members of a population (or rather their genomes: the strategies of their ‘selfish genes’, of which the individual is just the temporary vehicle). We may expect all organisms, including our own species, to be programmed to compete for differential reproductive success with their conspecifics, and for the resources and status positions which lead to the enhancement of reproductive success. But because our next-of-kin also bear replicas or copies of our own genes, natural selection will also favour those behavioural strategies which increase the reproductive success of our next-of-kin. This is called ‘kin-selection’, and is measured in terms of ‘inclusive fitness’, and its manifestation is nepotism or nepotistic altruism. A particular behaviour is ‘adaptive’ only in so far as it contributes to the organism’s inclusive fitness. It is rather easy to see that the concept of ‘preservation of the species’ has no evolutionary relevance whatsoever. Reproductive success of the individual organism is the only currency in the cold calculus of evolution.

From these basic considerations a number of other propositions can be derived. Inclusive fitness considerations also predict strikingly different reproductive strategies of the sexes (males competing with other males for the sexual favours and reproductive potential of females; females being coy, careful and choosy) and the conflict potential inherent in this (e.g. rape as an attempt to short-circuit the principle of female choice). Similarly sociobiological reasoning predicts a conflict potential in every area where there is a relative difference in coefficients of relatedness, and where the reproductive interests of individuals are not absolutely identical: parent-offspring conflict, sibling rivalry, conflict between the sexes (the ‘battle’ of the sexes), sexual competition and the ‘double standard’, ingroup-outgroup differentiation and ethnocentrism, and intergroup conflict along ethnic, ‘racial’, tribal, ideological and other cleavages.

Indeed, field observations of a great number of species have confirmed these sociobiological predictions: feticide, infanticide, siblicide, homicide, and rape, as the most extreme and gory forms of ‘conflict-resolution’, are much more widespread than was ever envisaged by the first generation of ethologists, such as Lorenz, who thought that animals had innate inhibitions against killing conspecifics, and that Man was a biological freak because he apparently lacked those inhibitions.

Basically, the sociobiological reasoning behind the ‘battle of the sexes’ is simple and straightforward: men and women invest differently in their reproductive success. For mammalian species, such as we ourselves are, female reproductive success is limited only by the amount of resources (time, energy, nutrients, etc.) she has to invest in offspring. But for the male, the female herself is the limiting resource: one male can inseminate many females and male reproductive success is only limited by the number of matings a male can achieve. Even in species where males typically invest in their offspring – and human males certainly do – the temptation of enhancing reproductive success by means of securing extra-pair

copulations and inseminating other females without further investment tends to select for a mixed male strategy of pair-bonding and philandering, and a female counter-strategy of carefully assessing the male's potential and willingness to invest in her offspring. Other consequences of this basic asymmetry in female and male parental investment will be considered in greater detail in the chapters to follow.

The Development (Ontogenetic Determinants) of Sex and Gender

Once the gametes from the mother- and the father-to-be have fused the resulting fetus normally displays chromosomal dimorphism (chromosomal sex: XX or XY) which influences the fetal gonadal sex: the undifferentiated gonad develops into testis or ovary.

In the case of a male (XY), the testicular secretions or hormones produced by the fetus are necessary for the continuing differentiation of the gonads and genitals in a male direction. The basic anlage (the 'default form') of the fetus/embryo is female, and unless counteracted by a Y chromosome and testicular hormones the embryo will further develop in a female direction. Maleness is, one could say, a deviation from this basic pattern. In the absence of testicular hormones the fetus will continue to differentiate and develop the reproductive anatomy of a female. Moreover, there is by now abundant evidence that these testicular secretions not only influence genital dimorphism but also have a priming effect on brain dimorphism, especially on those limbic and hypothalamic structures that will subsequently, much later in life, influence many aspects of sexual and agonistic behaviour. For the understanding of sex differences as discussed in this volume, it is important to realize that these sexually differentiated brains interact with the prenatal, perinatal and postnatal environment differently from the very beginning; they create/construct, as it were, a sexually dimorphic world. Normally, when no errors occur in this complicated, unfolding program – and many things can go wrong at every stage of the process: chromosomal mosaicism, (pseudo)hermaphroditism, gonadal dysgenesis, genital hypoplasia, female adrenogenital syndrome, male androgen insensitivity syndrome, to mention only the most frequent construction failures – girls and boys soon after birth develop stable body images and gender identities as either female or male, with a clear demarcation of the boundaries of the gender roles, and start their journey on the long and winding road toward puberty and adulthood. The surges of androgens during puberty have dramatic effects on the morphology and psychology of the maturing boy, while menarche and breast development have an equally dramatic impact on the girl-turning- woman. Androgen, especially testosterone, does not only affect aggressive behaviour in males, but also acts as the libido hormone in both men and women; thus there is evidence of a neurophysiological as well as an endocrinological interaction between the sexual and the agonistic behavioural systems in the males of the species. This pattern is very probably an ancient and general one in mammalian species, in which males commonly have to engage in vigorous agonistic interactions with other males in order to establish mating opportunities with one or more females.

> "Stated in nontechnical terms, the lesson from embryonic anatomy is that it is easier for nature to make a female than a male. The familiar embryonic and fetal rule is that something must be added to produce a male. Quite possibly, the same paradigm may apply also to gender-identity differentiation, though there is as yet no conclusive proof of this hypothesis". It would, however, help to explain why paraphilias (formerly called 'perversions') are almost exclusively male phenomena: "The majority of the paraphilias are found as distortions exclusively on man's gender identity, not woman's. Thus they

> provide still further evidence that nature has more difficulty in differentiating the gender identity of the male than the female. Nature makes more errors in the male" (Money & Ehrhardt, 1972).

For most men most of the time, sex is a short, sharp pleasure. For many women sex is a lifelong-lasting lamentable burden, or, at least, a nuissance, a curse of nature. For young adolescent males, sex (the 'fire of the loins') is more often than not a source of chronic frustration, but always fascinating to the point of obsession (One is reminded of Huxley's definition of an intellectual as someone who manages not to think of sex for full five minutes). For some young adolescent females sex is a horrifying prospect, or a commodity for exchange or exploitation, or a few minutes of agony for a bundle of joy, but rarely the exhilarating titillation it is to males. In romantic relationships sex is as often a source of traumatic conflict as it is of ecstasy and bliss. Relentless passion may ruin a love relationship, and vice versa.

There is evidently a wide experiential gap between the sexes. Many girls and women experience sex literally as violence, as a violation of their corporeal integrity, a penetration not only of the body but also of the personality and free will. For those women who are subjected to clitoridectomy, infibulation or pharaonic circumcision – a genital mutilation in which the clitoris is cut away and the vaginal labia have been sewn together in order to preserve the woman's virginity intact – sex is probably everything but a pleasurable experience once they have been cut open by their owner-husband. For the girls who have been sexually abused in their youths by adult males in power positions, or who have been raped, sex in later life is not an intimate, self-transcending sharing of mutual satisfaction but more probably a sordid traumatic affair, if, that is, they manage to engage in intimate erotic relationships at all.

For those women battered by jealous husbands or possessive lovers, it is probably of little solace to learn that the ultimate concern of the man involved is his 'confidence of paternity': Most wife beating and battering is the result of suspicion or knowledge of marital infidelity (Daly, Wilson & Weghorst, 1982), and as such it is part of the array of male anticuckoldry strategies; as is the universal double standard in matters sexual. – "The biological irony of the double standard is that males could not have been selected for promiscuity if historically females had always denied them the opportunity for expression of the trait" (R.L. Smith, 1984). Paradoxically, the same may be true for male homoeroticism, homosexuality and androgyny (Rancour- Laferrière, 1985).

Then why this suffering and conflict and frustration on account of sex? Why are we a sexually dimorphic species? Why are we a sexual species to begin with?

Sociobiology could be described as natural history – the evolutionary history of organic life – from the point of view of the genes. Genes are potentially immortal, while the organisms are merely temporary, mortal vehicles in the service of the replication of the genes. Many organisms, such as protozoans, have reproduced, and still reproduce, asexually, by means of fission or parthenogenesis, and they have been doing so successfully for millions of years. Then what is so special about ***sexual*** reproduction (needing two different morphs who each contribute only one half of their genes to the offspring): the way all animals best known to us, the mammals, and we ourselves do it? This question becomes especially enigmatic when we realize the costs involved in sexual reproduction. Sex is wasteful and inefficient: it uses energy, materials and time; and the highest cost of all is the damage, wounds and even death

incurred in the cut- throat competition for mates. What could the possible benefits be that transcend the substantial costs involved? Why did sex evolve? What do we mean by ‘sex’ in the first place?

What is ‘Sex’?

The term ‘sex’, as one might expect, is highly ambiguous and is used in a wide variety of meanings. In everyday parlance it usually refers to copulation (coitus) and its preliminaries and paraphernalia (which in the case of humans involve an extensive repertoire of play/pleasure components and erotic elaborations, e.g. mutual masturbation, fellatio, cunnilingus, etc. in the service of orgasm), and is equivalent to ‘making love’ or ‘sleeping together’ or ‘carnal knowledge’ or ‘doing it’ or ‘intercourse’ or ‘mating’ or ‘fucking’ or any other of the hundreds of euphemistic, clinical, legal or obscene terms we have invented to designate the genital union of two bodies. In contrast to the hedonic inventiveness of humans in matters sexual (carefully classified in such treatises as the ***Kama Sutra*** and ***The Perfumed Garden***), copulation is most animal species is a brusque “Wham bam, thank you Ma’am” affair (involving little affection or empathy, let alone love).

Besides this primary meaning of ‘sex’, we also use the term roughly as an equivalent of ‘gender’, male/female, masculine/feminine, as in ‘sex differences’, ‘sex roles’, ‘battle of the sexes’, etc.

In the third place, ‘sex’ is associated with the realm of vicarious gratification: wet dreams, masturbation fantasies, erotic imagery, in which we lustfully project what we would like to do to a particular person, or rather what we would like that particular person to want us to do to her/him. The ‘appeal’ in ‘sex appeal’ refers particularly to this meaning of ‘sex’.

And lastly, though we know reproduction to be result of sexual activity, it is not the first thing we usually associate with the term. The ***ultimate*** imperative of reproductive success has resulted in emphasis on the lustful components of the ***proximate*** behaviours, at least in humans and probably quite a number of primate species.

To an evolutionary biologist, however, the term ‘sex’ means quite different, and much less romantic and erotic, things. In the first place it refers to ***mixis*** (literally ‘mingling’): the reorganization, recombination or reshuffling of the genome. “It is readily apparent why this phenomenon might be inadequately distinguished from others that accompany it. Sex is often confused with reproduction. The two commonly go together, and the reason is that the occasion of producing a new organism is an appropriate time for producing one that is different” Ghiselin (1974) explains. And he continues: “The commonly used expressions ‘asexual reproduction’ and ‘sexual reproduction’ treat sex as if it were a subset of reproduction. We do have reproduction without sex: not only the usual sorts of vegetative growth, budding and fission, but also reproduction with gametes but lacking genetic recombination (amictic parthenogenesis). On the other hand we also have sex unconnected with reproduction – what might be called ‘areproductive sexuality’. This occurs in the ‘automixis’ of many protozoans... Likewise, the physical union of individuals is often confused with what will here be called ‘sex’ in the sense of recombination. Sex often means the genital intercourse of multicellular organisms, or the fusion of gametes or protozoa... For modern biology it is more important that we draw a distinction between sex and the more particular form of it called ‘amphimixis’... , or the formation of new kinds of genomes from

those of different individuals. Thus we have ***mixis*** and its two subclasses: ***automixis*** and ***amphimixis***" (Ghiselin, 1974).

It is by no means clear what exactly it is that we want when we want sex, when the libido is playing havoc with our peace-of-mind. Is it comfort and solace, escape from loneliness, relief of tension, acceptance, love, pair-bond, intimacy, body contact, lust, orgasm, erotic pleasure, satisfaction, tenderness, passion, ecstasy, romance, regression, hugging and caressing, mutuality, submission, conquest, dominance, or all of these in various combinations? In view of the many deceptive strategies and tactics men and women employ in their mating games, one might deduce that for males conquest, possession and control itself is a powerful incentive, while for females the intimacy of the relationship, which signals a long-term commitment, is prevalent in sexual satisfaction.

Why Did Sex Evolve?

The usual textbook answer to this vexing question is: "For the preservation of the species, of course". And, like so many textbook answers, it is wrong. The answer is based on the, still very 'en vogue', so-called 'group-selection' paradigm, which states in brief that something (in this case sexual reproduction) evolved because it was good, or advantageous, or functional, or adaptive for the group or the species. A recurrent problem with the group-selection paradigm is that something, be it somatic or behavioural, which evolves for the good of the individual organism always overrules that which may evolve for the good of the species (for technical details see NOTE 1). One example may suffice to illustrate this important principle of evolutionary biology: Induced abortions, intrauterine resorption of embryos, cannibalism and kronism of offspring, nest desertion and infanticide exist as evolved mechanisms and behaviours in many species. These mechanisms and behaviours can hardly be construed as good for the (preservation of the) species. Yet, they have evolved, and virtually all of these mechanisms and behaviours can be shown to be adaptive in terms of reproductive success, not for the species but for the individual organism practising them. So, once again, why did sex(ual reproduction) evolve if not for the good of the species?

Although some asexual species have apparently survived for very long times, this is not the general rule. Asexually reproducing species may well have immediate evolutionary advantages, but are less successful in the long run. The prevailing view is that asexual species are less able to keep up with environmental changes than are sexual ones.

The three arguments for the evolutionary advantages of sexual reproduction are (1) adjusting to a changing environment, (2) incorporating beneficial mutations, and (3) getting rid of deleterious mutations (Crow, 1988).

Why Only Two Sexes?

Biologically speaking, a female is by definition that sex that specializes in the production of a few, large, nutritious, and relatively immobile gametes (ova), while the male is by definition that sex that specializes in the production of a huge quantity of small, non- nutritious, motile gametes (sperm). Imagine an initial isogamic population in which individuals differ slightly in the size of gametes they produce. Some individuals will produce large gametes with high prospects of survivorship as zygotes, others will produce many smaller gametes with poorer

prospects of survival. Most individuals under the normal distribution curve produce intermediate gametes. With random fusion of gametes, such a system stabilizes over time – via a transient bimodal distribution – with mainly two genotypes (males and females) in a 1:1 ratio. As Parker (1984) explains: "The third genotype tends not to be represented either because it arises as the rather inviable product of the fusion of two 'proto- sperm' or because it is formed by the fusion of two 'proto-ova', depending on dominance. This latter fusion is rare because most gametes fuse with small gametes because of their numerical predominance. After several generations, the population is essentially anisogamous as a result of disruptive selection". This means that the final result of this process is the existence of two discrete and non-overlapping distributions of ovum-producers (females) and sperm-producers (males). In other words, the Evolutionary Stable Strategy (ESS) in this case is the stable coexistence of two morphs for gamete size. "Sperm producers survive by parasitizing the investment of ovum producers; the ESS solution (stable anisogamy) is essentially driven by sperm competition" (Parker, 1984). ("Oh God", my wife, who is reading over my shoulder, now cries out in desperation, "the feminists were right after all: males ***are*** parasites". And I shamefully nod).

But what if for whatever reason a third breeding morph arose in such a population, or that there would be three sexes: X, Y and Z, with mating patterns XZ, YZ, and XY? In that case a minimal selective advantage of one sex or zygote would eventually outcompete the others (simply by being more prolific), and again the final result would be two sexes.

Why is there a fifty/fifty sex ratio; why are there approximately equal numbers of each sex? This puzzle was in principle solved only in the 1930s by R.A. Fisher, and is accordingly called 'Fisher's principle'. When one sex numerically predominates in a population, it becomes advantageous for parents to invest in the opposite sex because that maximizes their offspring's reproductive success. With a preponderance of females, investment in males will ensure high opportunities for fertilization; and, conversely, with a preponderance of males, investment in females will produce the highest pay-off. This mechanism eventually stabilizes the sex ratio around 1:1. Fisher stated his solution in genetic terms, but the potential of parents to actually vary and manipulate the sex of their offspring may also be involved (Trivers-Willard hypothesis).

I am acutely aware that many people feel some kind of moral indignation, as if insult were added to injury, when their behaviour is compared to that of dragonflies, sticklebacks, rats or chimpanzees. "Man is the creature with culture and language and intelligence and free will", so the major objection goes, as if such Crown- of-Creation-argument would effectively invalidate or exclude any view of the human species as one species among a plethora of others, and having an evolutionary history just like the others. Selection thinking does not and cannot consider one species superior vis- à-vis others. For selection thinking or evolutionary theory ***Homo sapiens sapiens*** (as he calls himself somewhat arrogantly) is no more or less unique than other species.

The animal examples in this volume should be understood primarily as illustrations of principles, of strategies and solutions the genes have 'invented' or stumbled upon to solve common and recurrent problems of survival and procreation. If one reads that in a certain species females habitually cannibalize the males ***in copulo***, such a consumption pattern is not recommended for human females. Conversely, if one reads that in a certain species the males habitually rape the females of the species, that does not imply that such a strategy is recommended for human males either. It only means that in that particular species rape may

have evolved as one male counter-strategy to short-circuit the strategies of female choice. There is no moral stance or ethical precept involved.

The 'battle of the sexes' is, of course, a metaphor. But it is a metaphor based on a universal human experience: that there is not only harmony and peace and roses and honeymoons and bliss between the sexes, but also – and sometimes quite unintendedly and therefore the more mystifying ("Is it something I said?") – a lot of frontal collisions, misunderstandings, conflict, antagonism and even violence: intimate enemies on their own private, home-made battlefield. The clever reader might object that this is the universal human condition and not specifically confined to the relations between the sexes. And that is, of course, partially true. The evolution of anisogamy and it sequelae has, however, resulted in a whole new and specific category of potential conflicts over and above those which already plague an obligatorily social species such as we are. Not every battle is a 'battle of the sexes'. In this volume, Robin Russell and his colleagues from the university of London, United Kingdom, explore the variables which make for marital satisfaction.

Sociobiology has been accused of sexism (as a matter of fact is has been accused of every negative -ism which happened to be in fashion). But that surely must be a profound and tragic misunderstanding. Sexism is an ideology of discrimination on the basis of sex/gender, implying devaluation or inferiority of one sex vis-à-vis the other (for 'male chauvinist pigs' it is women who are considered the inferior sex; for particular breeds of militant feminism it is men who are considered to be subhuman 'scum' or worse). But there is nothing in sociobiology to warrant such an accusation. Superiority-inferiority considerations simply have no place in any science worthy of the name. To attempt to uncover sex differences and to try to explain these in terms of the different strategies which have evolved for the two sexes in the context of a long history of reproductive competition may be considered raving madness or sheer nonsense, but it is ***not***, and has nothing to do with sexism. (Sometimes the accusation is arrived at via a more convoluted route, which goes something like this: Sociobiology denies the exclusively sociocultural or environmental determination of sex differences and asymmetries, therefore it is responsible for the continuation of the situation of inequality, therefore it is conservative and/or reactionary, and therefore it is sexist. ***Quod erat demonstrandum***).

Sociobiologists are probably also more inclined than other social scientists to predict conflict, deceit and manipulation on all levels of existence: ethnic and other group conflict, male-female conflict, male- male conflict, female-female conflict, parent-offspring conflict, offspring-offspring conflict, even mother-embryo conflict and intragenomic conflict. But that, too, is a far cry from sexism. In this volume, Ullica Segerstråle, from the university of Chicago, U.S.A. discusses the sometimes troubled and ambivalent relationship of sociobiology and feminism.

Males are predicted to be sexually indiscriminate. Indeed, in many species the males will try to copulate with anything that even remotely resembles a female. Also the so-called 'Coolidge- phenomenon' (sexual habituation to the present mate, and strong arousal in response to the presence or anticipation of a potentially novel sex partner) points to the fact that males are selected to prefer diversity and variety in their sexual diet. "Small wonder that selection has favoured sex-crazed human males" (R.L. Smith, 1984). Such male indiscriminateness (simply because he can afford to), together with the fact, as we saw, that "Nature makes more errors in the male" may explain why vacuous, erratic, extravagant, non-reproductive, promiscuous, wanton and orgiastic sexual behaviour is virtually

exclusively a male ‘prerogative’; and why the three P’s (prostitution, pornography and paraphilias) appeal predominantly to men.

Females, in general, do not gain reproductively by such extravaganzas, and they are predicted to be extremely reluctant, coy, discriminate and selective in matters sexual, except in certain circumstances where relative promiscuity, or sequential polygamy or multiple matings may evolve as a strategy of female choice in the context of sperm competition and infanticide (e.g. in chimpanzees and barbary macaques (***Macaca sylvana***).

The power asymmetry between the sexes in all human societies we know (though some are much more egalitarian than others) is the most remarkable of all sex differences. Everywhere it is males trying to control the sexual and reproductive potential of females, and not the other way around. Women may exert considerable power behind the scenes, but the gladiators and the clowns in the political arena are males. Van den Berghe (1979) is undoubtedly the most acute analyst of this phenomenon. His work is highly recommended also for the reader who wants to make sense out of the wondrous world of matri- and patrilineality, in- and outbreeding, avuncu-, neo-, uxori- and virilocality, endo- and exogamy, dowry and brideprice, polygyny and monogamy; and how these phenomena, that have vexed anthropologists, can rather successfully be explained along sociobiological lines. In this volume Bobbi Low, from the university of Michigan, U.S.A, explores this power asymmetry in pre-industrial societies, while Vincent Falger, from the university of Utrecht, the Netherlands, explores the problem in modern, industrial societies.

R.L. Smith (1984) argued (following others) that continuous sexual receptivity in human females, cryptic or ***concealed ovulation***, and some other female anatomical peculiarities and feminine characteristics (such as the hemispheric, pendulous breasts, and menstrual synchronization) have evolved to obscure a human female’s current reproductive value and confuse males as a countermeasure to male resource allocation and anticuckoldry strategies. These female adaptations enhance opportunities for facultative polyandry and thus promote human sperm competition.

Most animals have regular patterns of mating (mating seasons) when copulation can result in pregnancy. This periodicity is usually synchronized between the sexes, and is mediated by hormones released in response to a variety of environmental stimuli.

Primates deviate from this typical mammalian pattern in that males occasionally copulate with infertile females. This behaviour is widespread among the primates (e.g. Hrdy, 1981) and is most highly developed in humans. Human females do not experience oestrus, offer no conspicuous morphological or behavioural evidence of ovulation, and are more or less continuously receptive to coitus from the onset of puberty.

Cryptic (concealed) ovulation and perennial sexual receptivity in humans has intrigued sociobiologists, and many have attempted to identify the ultimate causation of these phenomena. Most theorists have suggested that concealed ovulation and continuous female receptivity facilitate monogamous pair-bonding through the mechanism of permanent sexual attractiveness (cf. Alexander & Noonan, 1979).

In contrast, Benshoof & Thornhill (1979) proposed that concealed ovulation and continuous female receptivity evolved after female monogamy because any group-living female with inconspicuous oestrus in a monogamous mating system would be in a better position to mate

with a superior male without her being detected by her primary mate. Benshoof & Thornhill further suggest that ovulation is apparently concealed from the female because some degree of self-deception facilitates the deceit of mates.

Sexual Selection

> Sexual selection depends on the success of certain individuals over others of the same sex, in relation to propagation of the species; whilst natural selection depends on the success of both sexes at all ages, in relation to the general conditions of life. The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals... whilst in the other, the struggle is likewise between individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners (Darwin, 1871, p. 916).

This is how Darwin introduced the concept of sexual selection. The first kind of the sexual struggle is now better known as male-male and female-female competition. The second kind of the sexual struggle envisaged by Darwin is now known as epigamic selection or, simply, the principle of female choice. Darwin indicates the sexually dimorphic secondary sexual characteristics of many species, including humans, as the result of sexual selection. The gorgeous and exorbitant plumage of male birds-of-paradise, for example, is the result of such a kind of runaway sexual selection, based on the attractiveness to the females of the most exuberant-looking males. When sexual selection operates among males, adult males tend to become larger, heavier, showier, more competitive and better armed, and their behaviour patterns and ecological requirements tend to diverge from those of the females. This is one of the reasons why E.O. Wilson (1975) calls sex “an antisocial force in evolution”: it generates and multiplies conflicts of interests.

A whole array of traits is associated with the greater sexual competitiveness of males in a wide range of species. These include not only greater size and gaudiness, but also the price males have to pay for this: greater vulnerability and frailty in development, and shorter lifespans due to senescence, high risk-taking and mortality from fighting.

The ultimate basis of sexual selection is greater variance in mating success within one sex. In humans, for example, some powerful men may have many wives and children, while many poor, low-status men have neither. This differential in reproductive success underlies the formulation of Parental Investment Theory, developed by Trivers (1972), as outlined in the chapters to follow.

As may be seen from the bibliography at the end of this introduction (which covers only monographs and readers – excluding the many thousands of articles on the subject – and does not claim to be exhaustive), sex differences have been documented primarily by psychologists, psychoanalysts, anthropologists and feminist writers, long before sociobiology even existed. They are therefore not evil inventions by sociobiologists contrived in order to subordinate women, as I heard arguing recently. Sociobiologists have mainly added a new interpretation, a new framework for the understanding of the differences.

The conventional interpretation of these sex differences was in terms of differential learning, differential reinforcement, differential socialization, culturally-imposed sex role requirements

and restraints, sociocultural division of labour, and so on. But, as was already recognized by Archer (1976), such an interpretation does not address the following question: “The first is whether the nervous system of the developing child or of the adult, by being male or female, facilitates the learning of certain aspects of the appropriate sex role. The second related question concerns the evolutionary origin of the sex differences, whether they are the indirect consequence of adaptively significant biological sex differences of ancient origin”. (In 1976 this must have sounded like heresy). And a third question might be added: “Whether or not sex differences in behaviour are already apparent prenatally, and after birth are responded to differentially by the parents”.

Let us see what exactly was at stake, then and now. The following were – and still are – considered ‘established’ psychological sex differences:

Women show lower sensory detection thresholds than men for touch, pain, hearing, taste, smell, and scotopic (dark) vision, whereas men show lower thresholds for photopic (daytime) vision. Weiert Velle, from the university of Oslo, Norway, discusses these sex differences in sensory modalities in great detail. Hal Daniel, from the university of East Carolina, presents an experiment on differential perception of vocal sexiness.

Males are generally reported to show more ‘aggression’ than females, for measures of aggression taken during school life, and in laboratory measures of aggression taken in adulthood. Tore Bjerke, from the university of Trondheim, Norway, and Johan van der Dennen, from the university of Groningen, the Netherlands, will explore this crucial topic further in this volume. Men show faster reaction times when a simple motor task is involved, are more accurate in target-directed motor skills, and are faster on rotary-pursuit tasks.

Women perform better on tasks requiring more discrete or finely controlled motor responses and precision manual tasks, such as typing and other so-called ‘clerical skills’, and outperform men on perceptual speed.

Women show greater linguistic abilities (especially verbal fluency) from infancy onwards, and perform better on verbal IQ tests.

Men perform better in tests requiring judgment and manipulation of spatial relationships.

Men perform better on tests of mathematical reasoning ability, while women outperform men on tests of mathematical calculation.

Women are more highly attentive to sensory input and respond both to its emotional and socially meaningful properties.

Men are, in general, more object-oriented and achievement- oriented, while women are more socially-oriented, less competitive, and more nurturant.

Even when we cross the boundaries of what is considered normal, the sexes do so in different ways. Sex differences are striking in a number of psychopathological conditions. In childhood conduct disorders involving antisocial or destructive behaviour boys outnumber girls by far. Anxiety disorders and phobias are predominantly female, and animal phobias are almost

exclusively female. Psychopathy (sociopathy) is predominantly a male domain. In drug addiction and alcoholism males greatly outnumber females, etc. etc.

To these may be added the following cross-cultural observations (Rosenblatt & Cunningham, 1976), also quite well-known at that time:

Gender seems to be a basic distinction in many languages and possibly a basic distinction of social organization in all societies. In every society there is some division of labour by sex.

One task which may be at the root of many other sex differences in behaviour is childcare. Childcare is everywhere the duty of the child's mother. In some societies, older children, men and older people of both sexes may also have childcare duties.

In the search for calories, women in societies around the world bring in an average of roughly 30-40% of the caloric intake.

Warfare seems to be primarily an activity of men. No major society dominated by female warriors has been documented in the literature.

Cross-sex violence seems frequent during courtship in societies with relatively great freedom of choice of spouse.

Across the world it appears that men have higher public status than women. Men typically are the formally-recognized heads of domestic groups.

Women have power over men through their control of sexual relations with a mate and through the influence they have with their children and their natal kingroup.
As might be expected, there are also cross-cultural differences in the ways boys and girls are socialized.

(These are all, of course, general statistical statements which establish means and variances – with sometimes considerable distributional overlap – not statements about individuals, who may widely deviate from the mean, such that some men are more feminine in e.g. physical appearance than the average woman, and some women more masculine than the average man).

The point I want to make is that the various sex differences, from subtle perceptual ones to worldwide sociopolitical asymmetries, ***in toto*** make sense only in an evolutionary context, i.e., as a result of different selection pressures operating during the millions of years our ancestors lived in small kin-groups as scavengers-gatherers-hunters; fierce mating competition; sexual selection; and, very probably, a mutual 'arms race' of deceit- and detection-of-deceit-strategies.

An evolutionary view of sex differences in behaviour is not a relapse into the obsolete and acrimonious nature-versus-nurture debate. Rather, it provides a general framework for the attempt to understand them as consequences of different reproductive and parental investment strategies. How the sex differences arise and operate – whether genetically, congenitally, hormonally, socially or culturally acquired – and how saliently they are expressed, is rather immaterial from the point of view of the ultimate purpose for which they were designed by natural selection.

It is important to understand that an evolutionary vision of the human condition, as outlined here, does not deny the importance of cultural and socialization factors. There is no 'innate' rigidity or 'genetic determinism' implied. Firstly, because every trait is always expressed as an inextricable product of genotype and environment interaction. And secondly, our capacities for culture, language and learning (with all its inherent constraints) are themselves products of evolution.

After the contributions in this volume were written, in 1988 for the Oslo meeting of the European Sociobiological Society, a number of important books and articles appeared among which I recommend especially Lee Ellis: ***Theories of Rape: Inquiries into the Causes of Sexual Aggression*** (New York: Hemisphere, 1989), which presents an evolutionary theory of rape and discusses the (alleged) pornography-sexual violence relationship in meticulous detail. Martin Daly & Margo Wilson's ***Homicide*** (Hawthorne: Aldine de Gruyter, 1988) is a valuable source of information on the role of sexual competition and jealousy in male-male and male-female murder and criminal violence in general. Laura Betzig, Monique Borgerhoff Mulder & Paul Turke's (Eds.) ***Human Reproductive Behaviour: A Darwinian Perspective*** (Cambridge: Cambridge University Press, 1988) touches upon many of the subjects treated in this volume, as does Anne Rasa, Christian Vogel & Eckhart Voland (Eds.) ***The Sociobiology of Sexual and Reproductive Strategies*** (London: Chapman & Hall, 1989). One might also consult the research work by David Buss on conflict between the sexes a.o. in the ***Journal of Personality and Social Psychology***. Christopher Badcock's ***Oedipus in Evolution: A New Theory of Sex*** (Oxford: Blackwell, 1989) presents a valuable synthesis of evolutionary and Freudian ideas on human sexuality.

This volume is not going to make this a better world, or bring joy to mankind, but perhaps it might help in understanding each other a little better. Brillat-Savarin, famous gastronome, gourmet and connoisseur, said that the only enduring contribution to the happiness of mankind would be a delicious new recipe. Unfortunately, the contributors to this volume stumbled upon a career ***in academicis*** and not in the lucullian arts. I, for one, sincerely and humbly apologize for that.

The editor

Notes

1. The first problem with the traditional explanation in terms of group selection is, Stearns (1988) explains, that group selection – or in this case, selection of the attributes of ***species*** – does not work under most circumstances. The reasons for this are as follows:

(1) Selection pressure on a trait is proportional to the amount of variation in reproductive success among individuals that can be accounted for (a) by variation in the trait in question, divided (b) by the generation time (In this case, the variation would be between sexual and asexual individuals).

(1a) Generation times of individuals are much shorter than lifetimes of species – by a factor of 10,000 to 100,000 for most eukaryotes. Thus selection pressures on individuals are correspondingly much larger than selection pressures on species.

(1b) The response to selection depends on the amount of heritable variation available among the units selected. There is much more variation available for selection among individuals within a sexually reproducing species than there is among species within a lineage. Therefore the response to selection is much faster and larger for individuals than for species.

(2) Thus selfish individuals can always outcompete individuals that sacrifice their own interests to those of the species. If asexuality is an advantage to an individual, and sexuality an advantage to the species, then we should find that most organisms are asexual, for only rarely would the advantages of sexuality be so strong that species selection would overcome individual selection.

The second problem with the traditional view is that sex does seem to cost a lot. It should pay the individual to be asexual. For bacteria and single-celled organisms, the principal cost of sex is probably the time it takes to carry out recombination. This can lengthen the normal cell division time by a factor of two or more. All organisms encounter another cost of sex not related to anisogamy: recombination rearranges genotypes that have high fitness. Whenever selection is strong, this cost will be high, for by the fact of their survival all parents indicate their fitness in the local environment. In anisogamous species – all 'higher' plants and animals – the female provides cytoplasm to support the male genome. This results in the twofold cost of males, or cost of genome dilution.

Compare a sexually reproducing female with an asexually reproducing female. Suppose that all offspring cost the same amount in both cases. The sexually reproducing female has offspring that are half male, half female. The asexually reproducing female has offspring that are all female, each of which also reproduces asexually and replicates her entire genome. Because she produces twice as many female offspring, after, for example, five generations she should have 32 times as many female descendants, each of which will also contain a complete copy of her genome. Not only does the sexually reproducing female make only half as many female offspring per generation; each of them contains only half of her genome.

It was this cost that first convinced Williams (1975) that the prevalence of sexual reproduction poses a serious problem for evolutionary theory. The advantages of sex to the individual have to be very large if sex is to be maintained by natural selection in any population in which parthenogenesis can arise.

In practice, the advantage of being asexual is rarely twofold. In most animals the transition to asexuality is difficult. In small organisms the actual costs of sex are reduced by intermittent sexuality – a series of asexual generations followed by an occasional sexual generation. In large organisms, such as mammals and birds, the realized costs of sex are quite small because sexuality is fixed in these lineages. Because the asexual option is simply unavailable, mutant asexual competitors cannot invade.

The major contemporary hypotheses for the maintenance of recombination are:

The 'Tangled Bank' hypothesis: A whole family of models embodies the notion that the production of genetically diverse offspring is advantageous in an environment that is saturated, heterogeneous, or both. Ghiselin (1974) appears to have priority for this idea, which was further developed by Williams, Maynard Smith and Bell. Bell named it the Tangled Bank hypothesis, after the closing paragraph in Darwin's ***Origin***.

The 'Red Queen' hypothesis or Coevolutionary Arms Race (So called after Lewis Carroll's ***Alice in Wonderland***, in which the Red Queen has to run very fast in order to stay in the same place): The idea that recombination is an advantage in a coevolutionary race against competitors, predators, parasites and disease organisms has been brought up repeatedly. Disease organisms and parasites have a fundamental advantage in an evolutionary arms race. They can adapt themselves quickly to a specific host genotype. This brings the host population under strong frequency-dependent selection, for is pays to have a rare genotype during an epidemic.

DNA Repair Mechanism: The advocates of this hypothesis postulate that recombination evolved as a mechanism by which damage in one chromosome could be repaired by information in the homologous chromosome. This advantage was later followed by biochemical complementation between the homologous chromosomes that exploited the redundant information available in the diploid genome.

2. Crow (1988) summarizes the costs and disadvantages of recombination as follows:

1. Sexual reproduction is not very efficient qua reproduction. The time and energy required for meiosis and syngamy are substantial. As a means of multiplication, many asexual systems are more effective and less error-prone.

2. With anisogamy and separate sexes there is the cost of males. A female that could produce female progeny asexually with the same efficiency as by fertilization would have a twofold advantage.

3. With sexual reproduction selection acts on the genic or additive component of the genetic variance, whereas selection among asexual individuals acts on the genotypic or total genetic variance. If the genetic variances are the same, an asexual species can respond more rapidly to selection – at least for a limited time.

4. If dominance and epistasis are present, there may be segregation and recombination loads.

5. Free recombination does not provide a way for two or more rare genes that are individually deleterious, but collectively beneficial, to spread through a population.
6. There are well-established examples of situations in which there is a clear advantage in holding certain genes together. Sexual reproduction regularly breaks up favourable gene combinations.

3. The modes of sexual selection

I. Epigamic Selection

A. Based on choices made among courting partners

– 1. The choice among the different types of suitors is dependent on their relative frequencies

– 2. The choice is not frequency-dependent

B. Based on differences in breeding time: superior suitors offer to breed more at certain times than at others

II. Intrasexual Selection

C. Precopulatory competition

– 1. Differential ability in finding mates

– 2. Territorial exclusion

– 3. Dominance within permanent social groups

– 4. Dominance during group courtship displays

D. Postcopulatory competition

– 1. Sperm displacement

– 2. Induced abortion and reinsemination by the winning suitor

– 3. Infanticide of loser's offspring and reinsemination by the winning suitor

– 4. Mating plugs and repellents

– 5. Prolonged copulation

– 6. In 'passive phase' of courtship, suitor remains attached to partner during a period before or after copulation

– 7. Suitor guards partner but without physical contact

– 8. Mated pair leaves vicinity of competing suitors

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